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Paleontology and Geochronology of the Deseadan (late Oligocene) of Moquegua, Perú

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ABSTRACT

Subsequent to our initial reports of the discovery of Deseadan fossils in southern Perú, we have obtained new data regarding the paleontology and geology of the upper member of the Moquegua Formation. These data include newly recovered fossil specimens and further analyses of those collected in our earlier field seasons. We have also obtained an ash directly from within the fossil-bearing units near the summit of Cerro Pan de Azúcar. Biotites from this Sugarloaf ash give an age estimate of 26.25 ± 0.10 Ma, thus supporting our previous suggestion that these fossil-bearing horizons are of late Oligocene age (Deseadan South American Land Mammal “Age”) and removing our query regarding a possible early Miocene age. Most of the fossils are of notoungulates and most of these are trachytheriine mesotheriids. Remarkably, three distinct mesotheriid taxa appear to have been present in the Moquegua fauna, none of which are referable to the common *Trachytherus alloxus* of the nearby and at least partly contemporaneous Salla beds of Bolivia. Other fossils documented here include postcranial elements of the notohippid notoungulate, *Moqueguahippus*, a macraucheniid litoptern (cf. *Coniopternium*), an osteoderm of an unnamed species of armadillo (Dasypodidae, cf. Dasypodinae), and a claw of a phorusrhacid bird. We also describe a diminutive new hystricognath rodent, *Sallamys quispea*, sp. nov. It is similar to, but distinct from, *S. pascuali* of Salla. Indeed, despite the temporal and geographic proximity of Moquegua to Salla, none of the taxa from Moquegua that can be identified to species are known from Salla. Likewise, we have failed to find any dasypodids from Salla that have osteoderms like that described in this work. Thus, it appears that distinctive paleogeographic and

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paleoenvironmental conditions in the late Oligocene led to a regional biotic differentiation for the Moquegua area of coastal Perú.

INTRODUCTION

Upper regions of peaks west of the Río Moquegua, near the city of Moquegua (fig. 1), have yielded the first known fossils of the Deseadan South American Land Mammal “Age” in Perú (Shockey et al., 2006). Since preparation of the initial report of this discovery, additional data have been gathered

regarding the paleontology and geology of these localities in the upper member of the Moquegua Formation. The new data include additional specimens collected in subsequent fieldwork, further analyses of previously collected material, and ⁴⁰Ar-³⁹Ar geochronological analyses of an ash collected from directly within the fossil-bearing horizons near the summit of Cerro Pan de Azúcar (fig. 2).

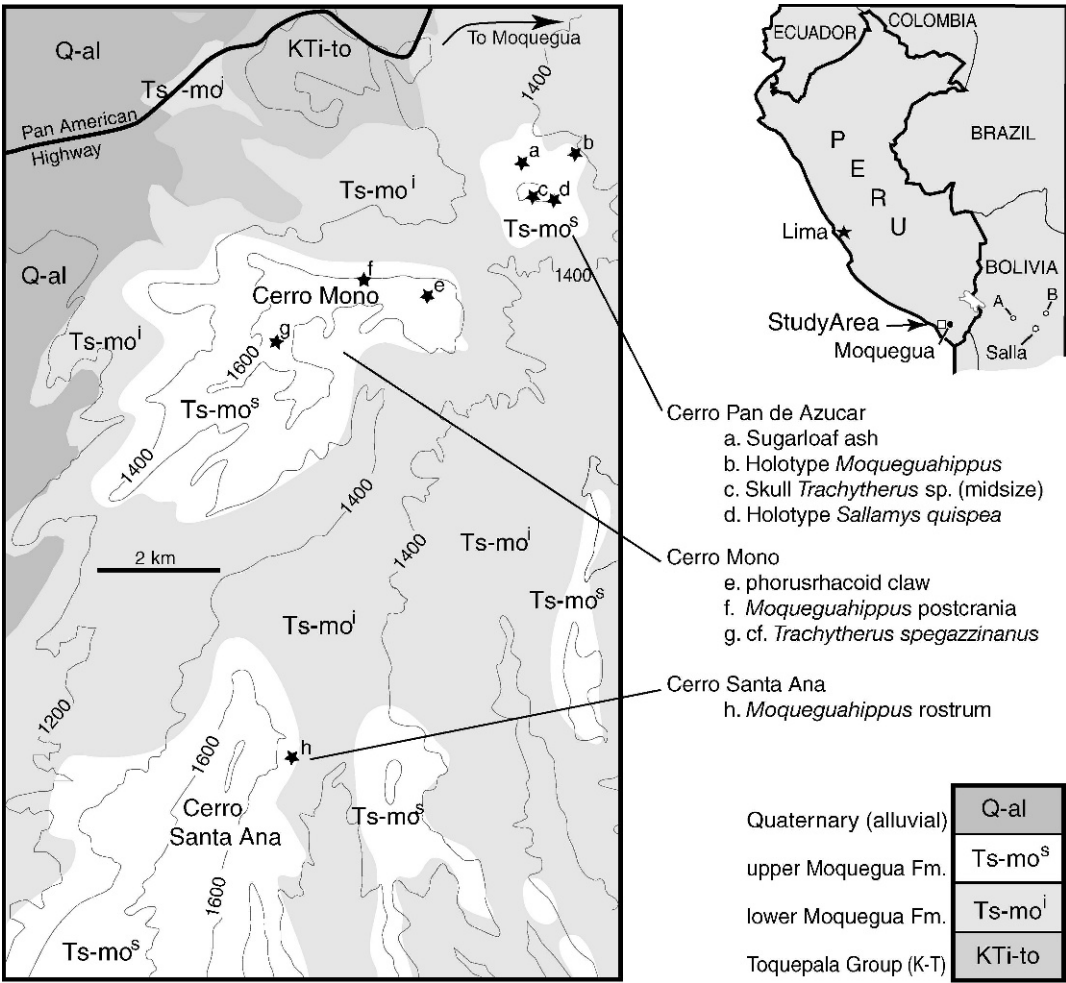


Fig. 1. Geologic map of the fossil localities of the upper Moquegua Formation. Based on: Bellido, E. and C. Guevara. 1961 (Mapa Geológico del Cuadrángulo de Clemensi, Carta Geológica Nacional y Instituto Geográfico Militar); Shockey et al., 2006: fig 1; and satellite images from Google Earth. Trachytherine localities of Bolivia are indicated in insert map at upper right: Salla (*Trachytherus alloxus*); A, Lacayani (*T. spegazzinianus*); and B, Río Iru Pluma (*T. subandinus*).

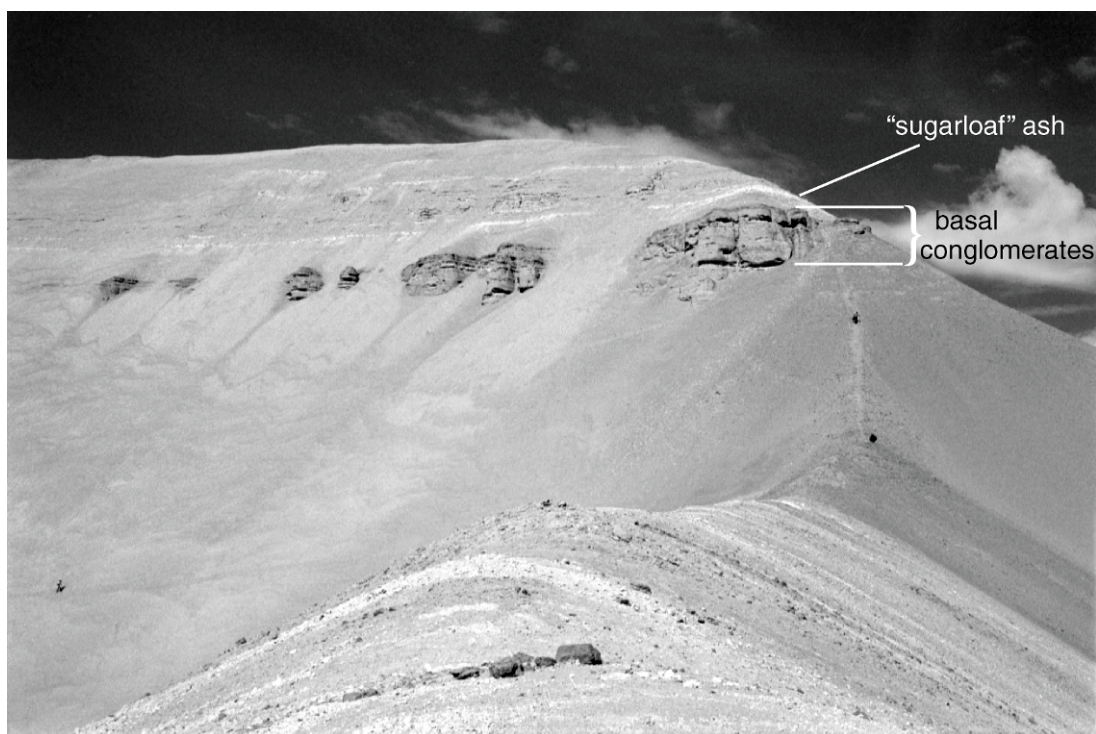


Fig. 2. Photo of the north face of the summit of Cerro Pan de Azúcar illustrating the lower region of the upper Moquegua Formation, including the Sugarloaf ash. (The boundary between the lower and upper Moquegua Formation is covered at this locale.) Note crew members hiking up the slopes for an impression of scale.

Most of the fossils recovered are of notoungulates. The present work describes postcranial remains from three species of mesotheriid notoungulates, including the nearly complete pes of the largest of the three (cf., *T. spegazzinianus*). This represents the first such description of any mesotheriid pes. Also, we describe additional material of the notohippid notoungulate, *Moqueguahippus glycisma* Shockey et al., 2006, and we expand the faunal list by reporting the remains of the only xenarthran (Dasypodidae, cf. Dasypodinae), and a diminutive new species of rodent, *Sallamys quispea*, closely related to but distinct from the Deseadan species *S. pascuali* from Salla, Bolivia.

As detailed below, the geochronological analysis provides a date of 26.25 ± 0.10 Ma for the ash that lies in the lower part of the fossil-bearing sequence. This date strongly supports the initial conclusion that the fauna collected is late Oligocene in age, thus

removing prior uncertainty regarding a possible early Miocene age for the fossil-bearing units (Shockey et al., 2006).

BACKGROUND

The Tertiary sediments in the Moquegua/Tacna Basin traditionally have been referred to as the Moquegua Formation (Bellido and Guerra, 1963) or Moquegua Group (Tosdal et al., 1981; Acosta et al., 2002), composed of the “formación Moquegua inferior” and the “formación Moquegua superior” (see Sempere et al., 2004, for discussion of nomenclature problems). These are separated by an angular unconformity (Acosta et al., 2002; Sempere et al., 2004); in addition, the “lower Moquegua Formation” consists of finer sediments than the upper.

Work in progress (see Sempere et al., 2004) may clarify the complex depositional history of the Tertiary deposits of southern Perú and

the resulting unstable geological nomenclature. The strata of interest for our study involve the upper unit of the Moquegua Formation (*sensu* Bellido and Guevara, 1963; Bellido and Landa, 1965; Tosdal et al., 1981; equivalent to: “Formación Moquegua Superior” of the Moquegua Group [Acosta et al., 2002]; “Formación Moquegua superior” [Flores et al., 2004] or “Upper Moquegua Formation” [Shockey et al., 2006]; “Moquegua C” [Sempere et al., 2004]; Moquegua Formation [Sánchez Fernandez et al., 2000]), underlain by the lower unit of the Moquegua Formation (equivalent to: “Formación Moquegua Inferior” of the Moquegua Group [Acosta et al., 2002]; “Formación Moquegua inferior” [Flores et al., 2004]; “Moquegua B” [Sempere et al., 2004]; Sotillo Formation [Sánchez Fernandez et al., 2000]). For convenience, given this conflict among various stratigraphic assignments, we will refer to the upper part of the Moquegua Formation as the “upper Moquegua Formation” and the lower part as the “lower Moquegua Formation.”

Bellido and colleagues (Bellido and Landa, 1965; Bellido and Guevara, 1963) characterized the Moquegua Formation as continental siltstones, sandstones, and conglomerates. Conglomerates form the base of the upper Moquegua Formation (fig. 2) with overlying finer-grained lagoonal facies (Tosdal et al., 1981; Acosta et al., 2002). These are composed of clayey and fine-grained sandstones and mudstones, with pink ignimbrite intercalations (Acosta et al., 2002). The regionally extensive lower Moquegua Formation locally unconformably overlies the late Cretaceous to early Tertiary Toquepala Group (Tosdal et al., 1981; Marocco and Noblet, 1990; Acosta et al., 2002; and fig. 1).

Tosdal et al (1981) obtained ^{40}K - ^{40}Ar dates (25.3 ± 0.8 , 23.3 ± 0.8 , and 22.7 ± 0.8 Ma) from three widely separated ignimbrite exposures near the top of the upper Moquegua Formation, all east of the Moquegua River. Our new dates (^{40}Ar - ^{39}Ar) come from an ash west of the Moquegua River, near the summit of Cerro Pan de Azúcar. This Sugarloaf ash lies just above the basal conglomerates, thus representing a stratigraphically older horizon than those sampled by Tosdal et al., 1981, for

their ^{40}K - ^{40}Ar geochronological analysis (see ^{40}Ar - ^{39}Ar Geochronology below).

The Moquegua Formation has generally been considered “nonfossiliferous” (Tosdal et al., 1981). However, in 2002, Rossana Quispe and her classmates and instructor (Jorge Acosta) from the Universidad Nacional “Jorge Basadre Grohmann,” Tacna, Perú, found fossils in the upper Moquegua Formation, at and just below the summit of Cerro Pan de Azúcar (Shockey et al., 2003, 2006). This initial discovery motivated our more intensive National Geographic-sponsored fieldwork in the austral winters of 2002 to 2004, with results detailed here.

MATERIALS, ABBREVIATIONS, METHODS

Specimens collected from the Deseadan aged localities of the upper Moquegua Formation are curated in the MUSM (Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Perú). Other institutional abbreviations used in the text include: UF (vertebrate paleontology collections, Florida Museum of Natural History, University of Florida, Gainesville, FL, U.S.A.); AMNH (American Museum of Natural History, New York, NY, U.S.A.).

Additional abbreviations used in this study include SALMA, South American Land Mammal “Age”; I, C, P, and M for upper incisors, canines, premolars, and molars, respectively (lowercase notation for lower teeth).

The ^{40}Ar - ^{39}Ar ages were obtained at the argon geochronology laboratory in the Department of Earth Sciences at the University of California, Santa Barbara. Conventional stepwise-heating and plateau-age analyses were conducted on biotite separates (Sugarloaf biotites) obtained from the ash collected above the basal conglomerates below the summit of Cerro Pan de Azúcar.

GEOGRAPHIC AND GEOLOGICAL CONTEXT

The Tertiary Moquegua localities lie 50 km inland from the Pacific in the coastal plains of southern Perú, east of the Cordillera de la Costa and west of the Cordillera Occidental of

TABLE 1
Analytical Data for $^{40}\text{Ar}/^{39}\text{Ar}$ for the Sugarloaf Biotites of Cerro Pan de Azúcar
Sample: SB51-18, Sugarloaf Biotite, $J=0.0020807$

T (°C)	t	40(mol)	40/39	38/39	37/39	36/39	K/Ca	Σ ^{39}Ar	$^{40}\text{Ar}^*$	Age (Ma)
650	12	1.6e-14	13.4769	1.9e-2	0.1618	0.0284	3.0	0.03529	0.377	19.0 ± 0.3
750	12	3.0e-14	9.1264	1.8e-3	0.0399	0.0082	12	0.13503	0.736	25.0 ± 0.1
820	12	2.0e-14	8.7735	3.5e-4	0.0351	0.0057	14	0.20587	0.807	26.4 ± 0.1
880	12	2.1e-14	8.6844	0.0e+0	0.0176	0.0053	28	0.28003	0.821	26.6 ± 0.1
940	12	2.3e-14	8.8685	0.0e+0	0.0136	0.0061	36	0.36067	0.798	26.4 ± 0.1
980	12	2.7e-14	9.6360	5.8e-4	0.0152	0.0085	32	0.44637	0.738	26.5 ± 0.1
1020	12	3.2e-14	9.4337	0.0e+0	0.0135	0.0081	36	0.55122	0.745	26.2 ± 0.1
1060	12	4.0e-14	8.6092	2.3e-4	0.0102	0.0055	48	0.69330	0.810	26.0 ± 0.1
1100	12	4.1e-14	7.9361	0.0e+0	0.0111	0.0030	44	0.85017	0.887	26.2 ± 0.1
1140	12	2.5e-14	7.6858	0.0e+0	0.0133	0.0022	37	0.95080	0.916	26.2 ± 0.1
1190	12	1.1e-14	7.6572	0.0e+0	0.0476	0.0018	10	0.99326	0.929	26.5 ± 0.2
1250	12	1.5e-15	9.2983	0.0e+0	0.2417	0.0062	2.0	0.99821	0.802	27.8 ± 1.3
1320	12	7.6e-16	13.0247	1.2e-3	0.2417	0.0229	2.0	1.00000	0.482	23.4 ± 4.0

Total fusion age, TFA= 25.90 ± 0.05 Ma (including J); weighted mean plateau age, WMPA= 26.24 ± 0.05 Ma (including J); inverse isochron age = 26.21 ± 0.17 Ma.; (MSWD = 4.52; $^{40}\text{Ar}/^{36}\text{Ar}$ = 297.8 ± 8.4); steps used: 820, 880, 940, 980, 1020, 1060, 1100, 1140, 1190°C, (3–11/13 or 86% Σ ^{39}Ar); t = dwell time in minutes; 40 (mol) = moles corrected for blank and reactor-produced 40; ratios are corrected for blanks, decay, and interference; Σ ^{39}Ar is cumulative, $^{40}\text{Ar}^*$ = rad fraction.

the Andes (fig. 1). These fossil-bearing beds of the upper Moquegua Formation are encountered only at the summits of a series of peaks (Cerro Pan de Azúcar, Mono, and Santa Ana) flanking the western banks of the Río Moquegua, which regionally runs along the W 71° longitudinal line in the Departamento de Moquegua, Perú. Cerro Pan de Azúcar is located 9 km WSW of the city of Moquegua, at S17°12.871' and W71°0.661' (elevation 1663 m). Cerro Mono (elevation 1780 m) stretches from 2 to 6 km SW of Cerro Pan de Azúcar, and Cerro Santa Ana (elevation 1790 m), S17°16.866' and W71°2.744', lies 10 km SW of Cerro Pan de Azúcar.

Intensive prospecting for fossils in the vast, but accessible, area of outcrop of the lower Moquegua Formation was entirely unproductive. All fossils found during our fieldwork came solely from the summits of the mountains where the upper Moquegua Formation is exposed. For the most part, the fossils were broken and scattered on the surface of the heavily weathered sediments.

^{40}Ar - ^{39}Ar GEOCHRONOLOGY: A volcanic ash ("Sugarloaf ash," in reference to its being from Pan de Azúcar [= *Sp. sugarloaf*]) is exposed on the north face of Cerro Pan de Azúcar, about 20 m below the summit and

20 m above the upper Moquegua Fm./ lower Moquegua Fm. contact (figs. 1: *a* on map; 2). A sample of this ash was collected at S17°13.016' and W71°0.786' and a 2.3 mg separate of biotites was subjected to a stepwise-heating ^{40}Ar - ^{39}Ar geochronological analysis. Each dwell time lasted 12 min at temperatures that ranged from 650° C to 1300° C. Plateau temperatures occurred at 820°, 880°, 940°, 980°, 1020°, 1060°, 1100°, 1140°, and 1190° C.

These data provided a total fusion age (TFA) of 25.90 ± 0.05 Ma (including "J," a summation term for a series of variables, determined by placing a "flux monitor" sample of known age in the reactor with the sample whose age is being determined, see table 1), a weighted-mean plateau age (WMPA) of 26.24 ± 0.05 Ma (including J), and an inverse isochron age of 26.21 ± 0.17 Ma (see table 1 and fig. 3). These yield a ^{40}Ar - ^{39}Ar age determination for the Sugarloaf ash of 26.25 ± 0.10 Ma. This late Oligocene age falls within the currently accepted time span of the Deseadan SALMA (Flynn and Swisher, 1995; Kay et al., 1998), and is consistent with the occurrence of Deseadan SALMA fossils that were all collected within about 20 m above the level of the ash or 10 m below, all within the upper Moquegua Formation.

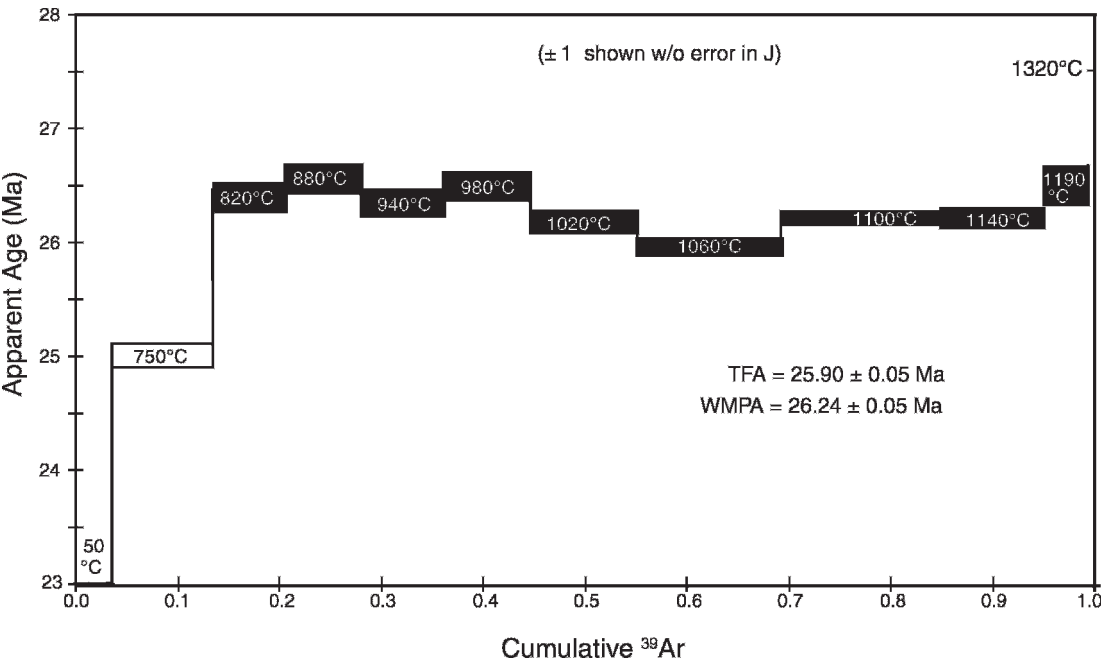


Fig. 3. Ar age spectra for the Sugarloaf biotite of Cerro Pan de Azúcar. TFA = total fusion age; WMPA = weighted mean plateau age.

This date of 26.25 ± 0.10 Ma from 20 m above the lower/upper Moquegua Formation boundary provides a radioisotopic age determination within the lower part of the upper Moquegua Formation. This date for the base of the upper Moquegua Formation is congruent with the younger ^{40}K - ^{40}Ar age determinations of Tosdal et al. (1981) for the upper part of the upper Moquegua Formation, which ranged from 22.7–25.3 Ma.

SYSTEMATIC PALEONTOLOGY

CLASS AVES LINNAEUS, 1758

FAMILY PHORUSRHACIDAE AMEGHINO, 1889

Genus and species indeterminate

Figure 4A

MATERIAL: MUSM 351, ungual phalanx, collected in the upper Moquegua Formation, near the eastern summit of Cerro Mono (fig. 1: e on map).

COMMENTS: Despite many hours of prospecting in the area where this avian ungual phalanx of was found, no further material of

this large bird has been recovered. Its presence at Moquegua was previously noted (Shockey et al., 2006) and we here provide a photo (fig. 4) of the single element from what must have been a moderately large bird.

In terms of its size, curvature, and presence of lateral nutrient grooves, the avian claw from Cerro Mono is similar to that of the Santacrucian (middle Miocene) *Phororhacos* (see Sinclair and Farr, 1932). It is not referred to *Phororhacos*, however, as it is a little smaller and has a lower degree of curvature. The material is inadequate to refer to any of the known Deseadan genera of phorusrhacid (e.g., *Physornis*, *Andrewsornis*, or *Psitopterus*; see Alvarenga and Höfling, 2003).

CLASS MAMMALIA LINNAEUS, 1758

MAGNORDER XENARTHRA COPE, 1889

ORDER CINGULATA ILLIGER, 1811

FAMILY DASYPODIDAE GRAY, 1821

CF. DASYPODINAE GRAY, 1821

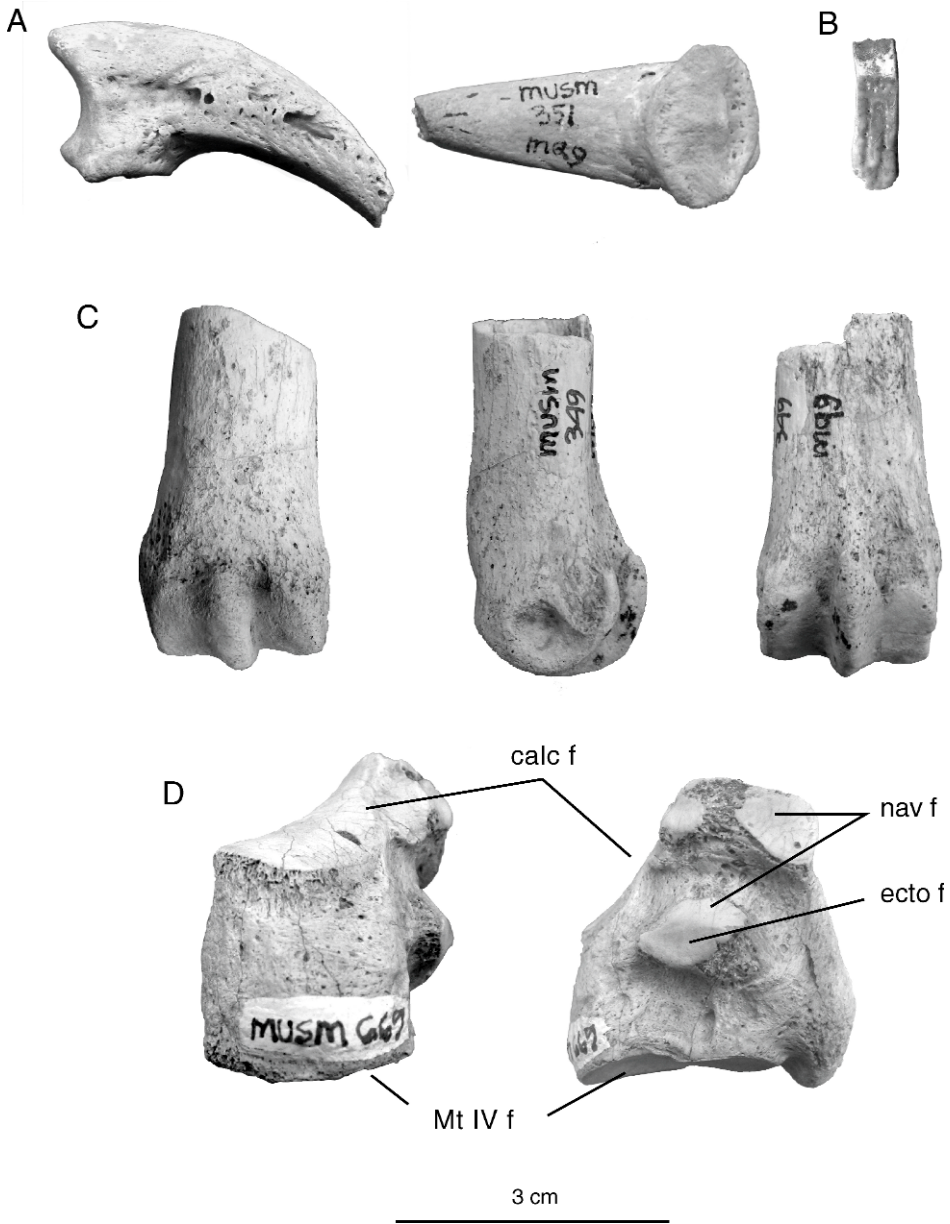


Fig. 4. Miscellaneous postcranial elements. **A**, phorusrhacoid claw (MUSM 351), in lateral and plantar views; **B**, dasypodid osteoderm (MUSM 1604) from the articulating region of the carapace; **C**, macraucheniid metapodial (MUSM 349) in dorsal, lateral, and plantar views; and **D**, right cuboid (MUSM 669) in dorsal and medial views.

Genus and Species Indeterminate

Figure 4B

MATERIAL: MUSM 1604, an isolated osteoderm, the anterior portion of which is

poorly defined. It was found in the upper Moquegua Formation, about 20 m below and southeast of the summit of Cerro Pan de Azúcar, in the area where the holotype of *Sallamys quispea* was found (fig. 1: *d* on map).

COMMENTS: MUSM 1604 is a movable-band osteoderm. It is rectangular, small, and slender, measuring 16.0 mm long and 4.7 mm wide. The lateral margins are smooth and fairly straight. The posterior border is slightly rounded; it is partly damaged, but five pits, likely sites for hair follicles, are recognizable. The central figure is delimited by two parallel sulci connected anteriorly and reaching the posterior margin. Each sulcus presents two large nonaligned foramina and a number of dispersed smaller ones. The articulation zone is well defined by a transverse bevel. As in some movable osteoderms of *Dasybus novemcinctus*, some foramina are identified just behind the bevel.

MUSM 1604 almost certainly represents a new taxon of a small Deseadan dasypodid, similar in size to *Dasybus hybridus*. Unfortunately, the scarcity of well-documented material of coeval taxa and the fragmentary condition of the present record discourages us from erecting a new species. It is probably a Dasypodinae based on the surface design of the osteoderm. The longitudinal and parallel sulci imply the existence of overlapping scales covering lateral areas of two adjacent scutes (secondary horny scales), an apomorphy for the Dasypodinae (Vizcaíno, 1994; but see Ciancio and Carlini, 2008). Its systematic position within the group is uncertain, though.

The Dasypodinae consist of the following tribes: Astegotheriini (including Stegotheriini; sensu McKenna and Bell, 1997) from the Paleocene to the Miocene (see Vizcaíno, 1994), and Dasypodini from the Miocene to the present (Vizcaíno, 1990; Carlini et al., 1997). Despite the vast expanse of time, general shape, and outline of movable osteoderms show little difference between both tribes. As in the Deseadan armadillo from Moquegua, they are thin and slender in Astegotheriini and Dasypodini (see Vizcaíno, 1994; Carlini et al., 1997). This conservative character was once used to diagnose the tribe Astegotheriini (Vizcaíno, 1994), but has since been regarded as representing a primitive state in the Dasypodinae evolution (Oliveira and Bergvist, 1998). The phylogenetic significance of the sutures of the margins is ambiguous, although they have implications regarding structural demands of the carapace. In MUSM 1604 the

margins are smooth, similar to what is seen in the Astegotheriini. Vizcaíno (1994) suggested that in these animals the carapace was more flexible than in modern Dasypodini where the scutes are fixed by spicules along their lateral margins. The osteoderms of archaic Astegotheriini and the Dasypodinae from Moquegua may have been bounded together by soft tissue.

In most Astegotheriini from the Casamayorian-Mustersan of Patagonia (e.g., *Astegotherium*) the main figure is lageniform and the sulci do not reach the posterior margin (see Vizcaíno, 1994). In *Anadasypus hondanus* from the Middle Miocene of La Venta (Colombia), parallel sulci diverge laterally to reach the sides just before getting to the posterior margin. It is considered the oldest member of the Dasypodini because this pattern suggests the derived state seen in extant species of *Dasybus*, in which the secondary keratin scutes are triangular (Carlini et al., 1997). In the osteoderms, the synapomorphy is revealed by the divergent sulci that reach each posterolateral corner (Vizcaíno, 1990). In the dasypodine from Moquegua, surface design of the osteoderm implies (1) secondary horny scales were rectangular—not triangular and (2) each secondary scale took up the total length of the visible surface of the osteoderm. This combination of characters is not seen in the early members of the Astegotheriini, but it may have been attained and by a cluster of a pre-Dasypodini during the Oligocene.

ORDER RODENTIA BOWDICH, 1821

SUBORDER HYSTRICOGNATHA TULLBERG, 1899

SUPERFAMILY OCTODONTOIDEA SIMPSON, 1945

GENUS *SALLAMYS* HOFFSTETTER AND LAVOCAT,
1970

Sallamys quispea, sp. nov.

Figures 5 and 6; table 2

HOLOTYPE: MUSM 1404, jaw fragment with lower right dp4-m1.

REFERRED SPECIMENS: Known only from the holotype.

TYPE LOCALITY: The upper Moquegua Formation, about 20 m below and southeast

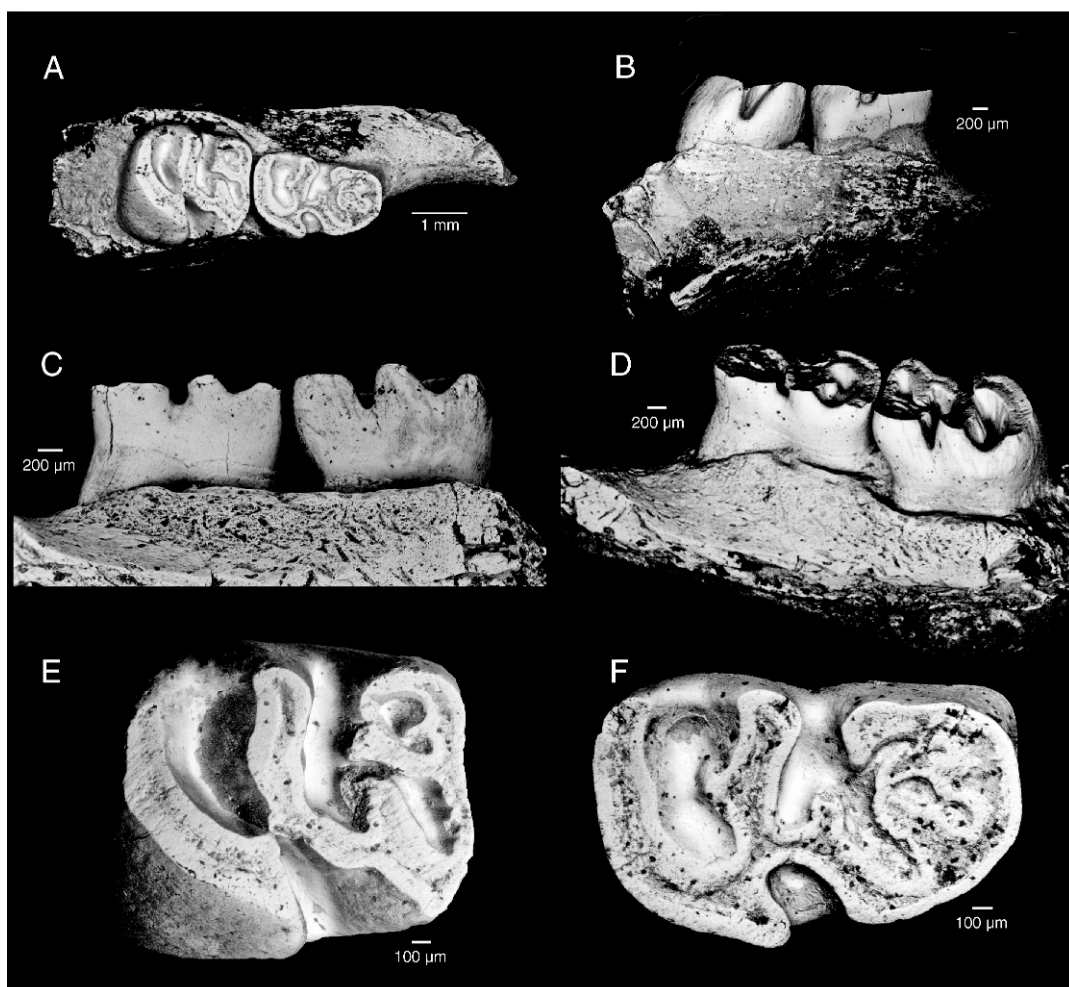


Fig. 5. Holotype of *Sallamys quispea*, MUSM 1404. Micrographs provide views from four perspectives (occlusal [A], lateral [B], medial [C], and medial oblique [D]) as well as close ups of the occlusal surfaces of m1 (E) and dp4 (F).

of the summit of Cerro Pan de Azúcar (fig. 1: *d* on the map).

ETYMOLOGY: The specific name, *quispea*, is given to honor Rossana Quispe of the city of Moquegua, who discovered the first fossils known from the Moquegua Formation. She also participated in all our field projects in the Moquegua Formation, during one of which she found the holotype of this diminutive rodent.

DIAGNOSIS: Smaller than all known Deseadan and Santa Rosa local fauna (Perú) rodents, slightly smaller than the smallest known specimens of *Sallamys pascuali*;

brachydont; trilophate m1 with occlusal connection of the posterolophid to the hypolophid, mesolophid extending from the ectolophid; metalophid intersecting midpoint of anterolophid. The m1 anterolophid has a spur that with more wear would subdivide the fossetid into two. The m1 is subquadrangular, whereas dp4 is more ovoid. Molariform dp4; hypolophid with a small, posteriorly extending spur; anterolophid extends from protoconid around the anterior end of tooth to the metaconid, so that the anterolophid spur and metalophid tip join to form a figure eight-shaped fossetid.

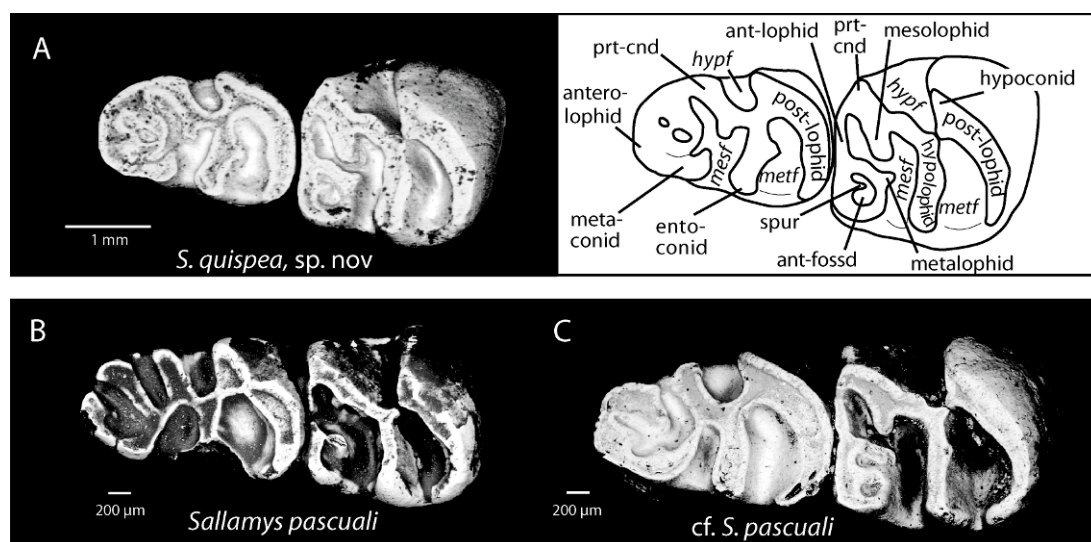


Fig. 6. Comparative anatomy of dp4 and m1 of *Sallamys* spp. **A**, Right dp4 and m1 of *S. quispea*, sp. nov. (holotype, MUSM 1404), shown as a SEM micrograph (left) and a line drawing (right) to illustrate the terminology used in the text. (Terminology based on Patterson and Wood, 1982; and Candela, 1999: Abbreviations: *hypf* = *hypoflexid*; *hyp-lophid* = *hypolophid*; *mesf* = *mesoflexid*; *post-lophid* = *posterolophid*; *prt-cnd* = *protoconid*.) **B**, is the right dp4 and m1 of PU 20909, *Sallamys pascuali*, in which the dp4 reflects the morphology of that of the holotype (Hoffstetter and Lavocat, 1970). **C** is a left dp4 and m1 (digitally reversed to appear as right) of *Sallamys*, cf. *S. pascuali*, UF 114458, in which the morphology of the dp4 is distinct from that of the holotype and referred specimen PU 20909 (see Patterson and Wood, 1982: fig. 5d, and text for discussion). Photo of PU 20909 © Yale Peabody Museum of Natural History, New Haven, Connecticut.

DIFFERENTIAL DIAGNOSIS: *Sallamys quispea* differs from rodents of the Deseadan assemblage from Salla, Bolivia, in the following ways: It is most similar in overall morphology to *Sallamys pascuali*, but with lower crown height; dp4 not as molariform, but subequal in size to m1 (just 3% longer than m1 in mesiodistal dimension), whereas dp4s of *S. pascuali* are larger (14%–25% longer than m1); anterior lophid of dp4 continuous from protoconid to metaconid, lacking the flexid that separates protoconid from anterior lophid of *S. pascuali* and lacking a second mesiolabial flexid; mesolophid of dp4 without connection to metaconid; less pronounced recurvature of lingual extreme of posterolophid of dp4 and m1; posterior spur at hypolophid-ectolophid junction of m1 shorter. Dental dimensions smaller than those of *S. pascuali* (mesiodistal dimension of dp4 just 82% that of smallest dp4 of *S. pascuali* and m1 mesiodistal dimension similar to that of only the smallest of individual sampled of *S.*

pascuali, but with transverse dimension shorter than all). Differs from *Branisamys luribayensis* in its much smaller size (m1 mesiodistal dimension just a third of that of *B. luribayensis*); m1 having only three major lophids, mesolophid not distinct or fully formed. Differs from *Incamys bolivianus* in smaller size (linear dimensions 40%–65% of those of *Incamys*); labial hypolophid and posterior lophid of m1 closer, forming a united crest with little wear (persistently separated in *Incamys*); lingual spurs projecting from antero-lophid of m1 with formation of an anterofossetid. Differs from *Migraveramus beatus* in having only three major lophids (mesolophid short, not reaching the metaconid), wider meta- and mesoflexids, and considerably smaller size (m1 mesiodistal dimension less than 75% to those of *M. beatus*).

Sallamys quispea differs from rodents of the Deseadan of Patagonia: Differs from *Platypittamys* in more complex antero-lophid, two anterofossetids. Differs from *Deseadomys aram-*

TABLE 2
Measures (mm) of the dp4 and m1 of Holotype (MUSM 1404) of *Sallamys quispea* sp. nov. of Moquegua, Perú, Compared to Those of *Sallamys pascuali* of Salla, Bolivia
Data of Yale Peabody (PU) specimens are from Patterson and Wood, 1982.

Taxon	Tooth	Mesiodistal (A/P) length	Greatest width	Height
<i>Sallamys quispea</i>	dp4	1.80	1.25	1.0
	m1	1.75	1.70	0.85
<i>Sallamys pascuali</i>				
	UF 114458	dp4	1.80	1.20
		m1	2.20	1.30
	UF 114756	m1	1.95	1.05
	UF 114759	m1	2.05	1.45
	UF 114837	m1	2.05	1.45
	UF 92802	m1	1.90	1.45
	UF 92805	m1	2.30	1.50
	UF 114455	m1	1.80	1.10
	UF 121163	m1	2.00	1.20
	UF 114484	m1	1.90	1.25
	PU 20907	m1	1.92	—
	PU 20908	m1	2.01	—
	PU 20909	dp4	1.47	—
		m1	2.03	—
	PU 20910	m1	2.06	—
	PU 20912	m1	2.15	—
	PU 21950	m1	1.97	—

bourgi by hypolophid more parallel to borders of occlusal surface and having additional anterofossetid. Differs from *Deseadomys loomisi* by presence of mesoslophid and semblance of metalophid. Differs from *Scotamys* by complexity of lobes and lack of cementum. Differs from *Cephalomys* by short hypoflexid, longer metaflexid and mesoflexid, brachydonty. Differs from *Asteromys punctus* by its much lower crown height, shallower flexids, and its much smaller size.

Differs from all known Santa Rosa local fauna rodents (*Eosallamys*, *Eoespina*, *Eodelphomys*, *Eoincamys*, *Eobranisamys*, *Eopicure*, *Eopululo*, *Eosachacui*) by m1 lacking a third fossetid of nearly equal length and depth, a feature characteristic of all members of the “Santa Rosa local fauna” rodent assemblage (Frailey and Campbell, 2004).

DESCRIPTION: Among Deseadan rodents (and those from the uncertain age Santa Rosa local fauna), *Sallamys quispea* is closest in size and morphology to *Sallamys pascuali*, falling just below the lowest part of the size range of dental measures of specimens of *S. pascuali* from Salla (see table 2 and differential

diagnosis above). Our study of a sample of small rodents from Salla referred to *S. pascuali* illustrates that that species is quite variable morphologically (assuming that all of these teeth indeed pertain to a single species). One dp4 (PU 20909; fig. 6B; see also Patterson and Wood, 1982: fig. 5d) has a discontinuous anterolophid separated from the protoconid by a flexid and further divided by an anterolabial flexid near the mesial apex of the tooth. Unlike that of *S. quispea*, the anterolophid connects to the mesolophid in the Bolivian specimens (PU 20909 and in UF 14458). The UF specimen, however, lacks the anterolabial flexid near the mesial apex as occurs on PU 20909. The wear pattern in both morphs is similar to that of the new Moquegua species of *Sallamys* in which the labial side wears more quickly than the lingual in both m1 and dp4. The mesiolingual end of the m1 of the Salla and Moquegua specimens have an “E” formation, made up of the tip of the anterolophid, a spur, and a short metalophid. In *Sallamys quispea*, however, the tip of the anterolophid joins with the metalophid rather than with the spur.

The m1 of *Sallamys quispea* has a distinct, but short, mesostylid, as does UF114759 (absent in PU 20909), but the m1 of the new taxon still is more complex in the anterior end of the molar than in the comparative specimens of Salla. The posterior side of the hypolophid is undulating in the new species. It is unlikely that *S. quispea*, at the same wear stage, would resemble UF 114759 and maintain a similar depth in its flexids (as in UF 114759).

COMMENT: Patterson and Wood (1982) considered the flexids of the dp4 of diagnostic significance for the genus *Sallamys*; that is, species of *Sallamys* should be recognizable by the presence of two labial, one mesiolabial, and two lingual flexids. The absence of the mesiolabial flexid in at least one Salla specimen of *Sallamys* (UF 114458) and in *S. quispea* (which also lacks the labial flexid between the protoconid and anterolophid) indicates that the flexid number of the dp4 is an unreliable means of recognizing the genus *Sallamys* and apparently even the species *S. pascuali*.

ORDER LITOPTERNA AMEGHINO, 1889

FAMILY MACRAUCHENIIDAE GERVAIS, 1855

Genus and Species Indeterminate
(cf. *Coniopternium* sp.)

Figure 4C, D

MATERIAL: MUSM 669, edentulous and damaged left mandibular ramus and right cuboid, found in slump below the conglomerates that form the base of the upper Moquegua Formation at the western flanks of Cerro Pan de Azúcar; MUSM 349, distal metapodial from the eastern summit of Cerro Mono.

COMMENTS: The metapodial (fig. 4C) is asymmetric and has a strong keel, thus representing one of the supportive metapodials (Mc II or IV; or Mt II or IV). Its distal keel is well developed, especially on the plantar surface where it is tall and bladeliike. Unlike metapodal IIIs of macraucheniids (Loomis, 1914: fig. 10; Shockey, 1999) the keel extends to the dorsal surface; however, it does not rise as high as that on the plantar

side. The distal width is 18.2 mm, which is about the size of a similar element from Salla, cf. *Coniopternium* sp. (UF 173216), which has a distal width of 19.4 mm.

The cuboid (fig. 4D) is similar to that of *Coniopternium andinum* described and figured by Loomis (= *Notodiaphorus crassus* of Loomis, 1914: fig. 12). The apex of our specimen is damaged, thus obscuring any astragalar facet as noted by Loomis (1914) and Shockey (1999) for *Coniopternium*. The Mt IV facet is 17.0 mm wide and 21.1 mm deep. In distal view it is pear shaped, with the apex directed to the plantar side and widest dimension near the dorsal surface.

As known so far, the macraucheniid of Moquegua is not distinct from comparable material representing *Coniopternium* spp. from Salla, but it is too small to be referred to the Patagonian species, *C. andinum*. Unfortunately, diagnostic elements for *Coniopternium*, such as dentitions or the calcaneum, are lacking, so we must remain uncertain as to even the generic taxonomic reference of the macraucheniid of Moquegua.

ORDER NOTOUNGULATA ROTH, 1903

SUBORDER TOXODONTIA OWEN, 1853

FAMILY (PARAPHYLETIC) NOTOHIPPIDAE
AMEGHINO, 1894

Moqueguahippus glycisma
Shockey et al., 2006

Figure 7 and table 3; Shockey et al.,
2006: fig. 3

MATERIAL: Holotype, MUSM 348, left mandible with p1–3 (p4 and m1 missing) and m2–3, discovered by Rossana Quispe and colleagues at Cerro Pan de Azúcar (fig. 1: *b* on map); and the following referred specimens: MUSM 676, left premaxilla with fragment of anterior maxilla with damaged and or badly worn anterior teeth: I2, I3, dC and C, dP1, and dP2 and P2, found at Cerro Santa Ana by Eucebio Diez (fig. 1: *h* on map); and MUSM 964 associated postcranials, including left astragalus, distal humerus, left proximal radius, unciform, left Mc III, and proximal end of Mc II (?) found by Walter Aguirre atop the east-west ridge between the

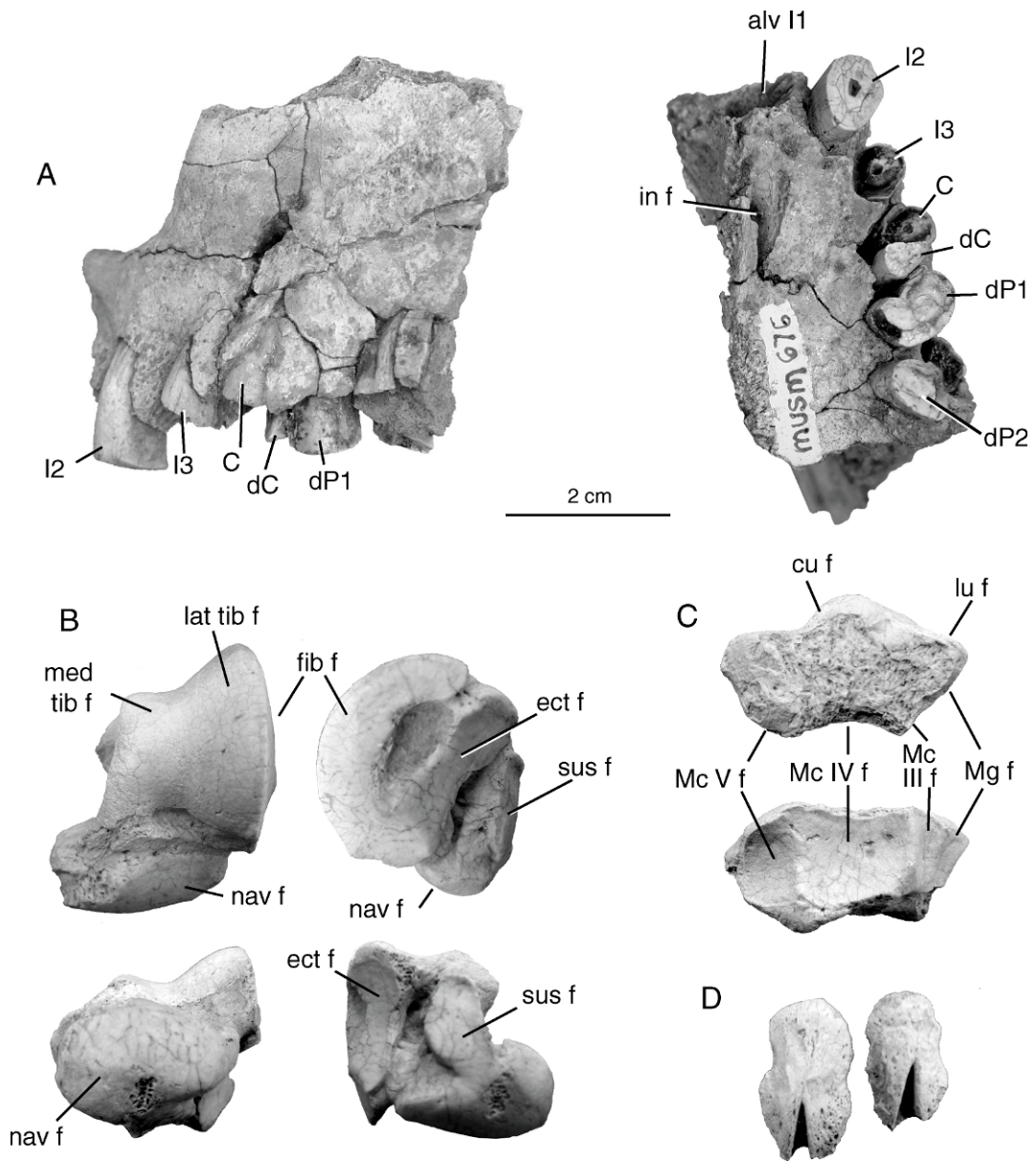


Fig. 7. *Moqueguahippus glycisma*. A, MUSM 676, (left) left rostrum with I2-3, dC, C, dP1 and P2; (right) close up of dentition; and MUSM 964: B, left astragalus in (clockwise) dorsal, lateral, distal, and plantar views; C, right unciform in dorsal and distal views; and D, two manual ungual phalanges in dorsal view.

two major summits of Cerro Mono at S17°13.835' and W71°2.020' (fig. 1: f on map).

DESCRIPTION: *Moqueguahippus glycisma* is distinguished from other notohippids by its unique character complex that includes its relatively large size, absence of entolophid fossettids of lower molars, presence of cemen-

tum over the teeth, and distinctive lower premolar morphology (Shockey et al., 2006). *Moqueguahippus* had previously been known from the holotype only, but new material provides some information regarding the upper dentition and a few details of its postcranial skeleton.

TABLE 3

Measures (mm) of Astragalus of *Moqueguahippus glycisma*, MUSM 964, from Cerro Mono, Moquegua

Astragalus (proximodistal)	32.7
Astragalus (trochlear width)	17.8
Astragalus (width max)	20.0
Astragalar head (transverse)	20.5
Astragalar head (dorsoplantar)	13.5

Based on its size and by the cementum present on the teeth (fig 7A), MUSM 676 is referred to *Moqueguahippus*. It is a portion of the muzzle of a subadult in the process of shedding its milk teeth just as the adult C and P2 are erupting. It apparently had no diastema as there are no gaps between any of the teeth between I1–P2. The general form of the muzzle indicates that it was rounded, similar to that of *Rhynchippus equinus* and *Eurygenium pacegnum*, but unlike that of *Eomorphippus obscurus* and *Pascualihippus boliviensis*, (see Simpson, 1967, and Shockey, 1997, respectively) which have broad premaxillary regions with transversely linear incisive batteries. Owing to wear and breakage, none of the crowns of the teeth are preserved.

The I1 is missing and the crowns are broken from I2–3. The premaxillary/maxillary suture between I3 and the canines (C and dC) is distinct and (in palatal view) extends medially to the distal most point of the incisive foramen. The incisive foramen is teardrop shaped, almost entirely enclosed by the premaxilla. The C is erupting just anterior and lateral to the heavily worn dC. The crown of the C is broken and that of the dC broken at the anteriolabial quadrant. The dP1 is reniform in occlusal view and is so heavily worn that no crown topology is seen. As is typical, but not universal in notohippids, the dP1 does not seem to be replaced (we observe an exception in FMNH P 13410 *Rhynchippus equinus* in which both the dP1 and P1 are present). The dP2 is unusual in that it is smaller than dP1. The erupting P2 is broken, leaving no hint of its form, other than that it, too, was relatively small.

MUSM 964 includes various postcranial elements found in close association. The most instructive elements are of the pes and manus.

The astragalus of *Moqueguahippus* (fig. 7B) has extremely asymmetric trochlear ridges,

similar to that of *Trachytherus*. It differs by its short neck, broad head, lack of a peronial process, and by its more parallel lateral and medial sides whereas those sides are oblique in *Trachytherus*, giving a greater transverse dimension to the plantar surface than the dorsal. The head of the astragalus of *Moqueguahippus* is unusually broad. The transverse dimension of the head (20.2 mm) is greater than the width of the trochlea (17.2 mm). The sustentacular facet grades into the broad articular region of the head. The ectal facet does not lie on the same plane as the sustentacular facet, but is oblique to it, having more of a vertical component to it.

Only a portion of the tuber of calcaneum was found among the remains of MUSM 964. However, the distal fibula has a flat distal articular surface, nearly perpendicular to the vertical astragalar facet, indicating that there was significant contact and articulation between the fibula and calcaneum.

The unciform (fig 7C) is distinct from that of *Trachytherus* in that the ulnar side is large and articulated with the Mc V, whereas the ulnar side of *Trachytherus* is tapered and there is little to no unciform–Mc V contact (see fig. 8 A–C). The unciform of *Moqueguahippus* is similar to that of *Eurygenium pacegnum* (Shockey, 1997: fig 4b), but not as deep as that of *Rhynchippus equinus* (Loomis, 1914: fig. 59). The Mt V facet is not as vertically oriented as that of *Rhynchippus*, which has a very reduced Mt V.

The only complete metapodial appears to be Mt II. It is 56.3 mm long with a proximal end having a transverse dimension of 14.6 mm. This proximal region is fairly complex, having articular surfaces that presumably overlapped Mt III and articulating with the meso- and ectocuneiforms. A lateral articulation may have served as an articular joint for the endocuneiform or possibly a Mc I.

A couple of distal phalanges were among the remains of MUSM 964 (fig. 7D). They are likely phalanges of the manus, as they are grossly similar to those of several Tertiary notoungulates, including the toxodontid *Adinotherium*, the notohippids *Eurygenium* and *Rhynchippus*, and the mesotheriid *Trachytherus*. These, like those of *Trachytherus*, have a longitudinal distal fissure.

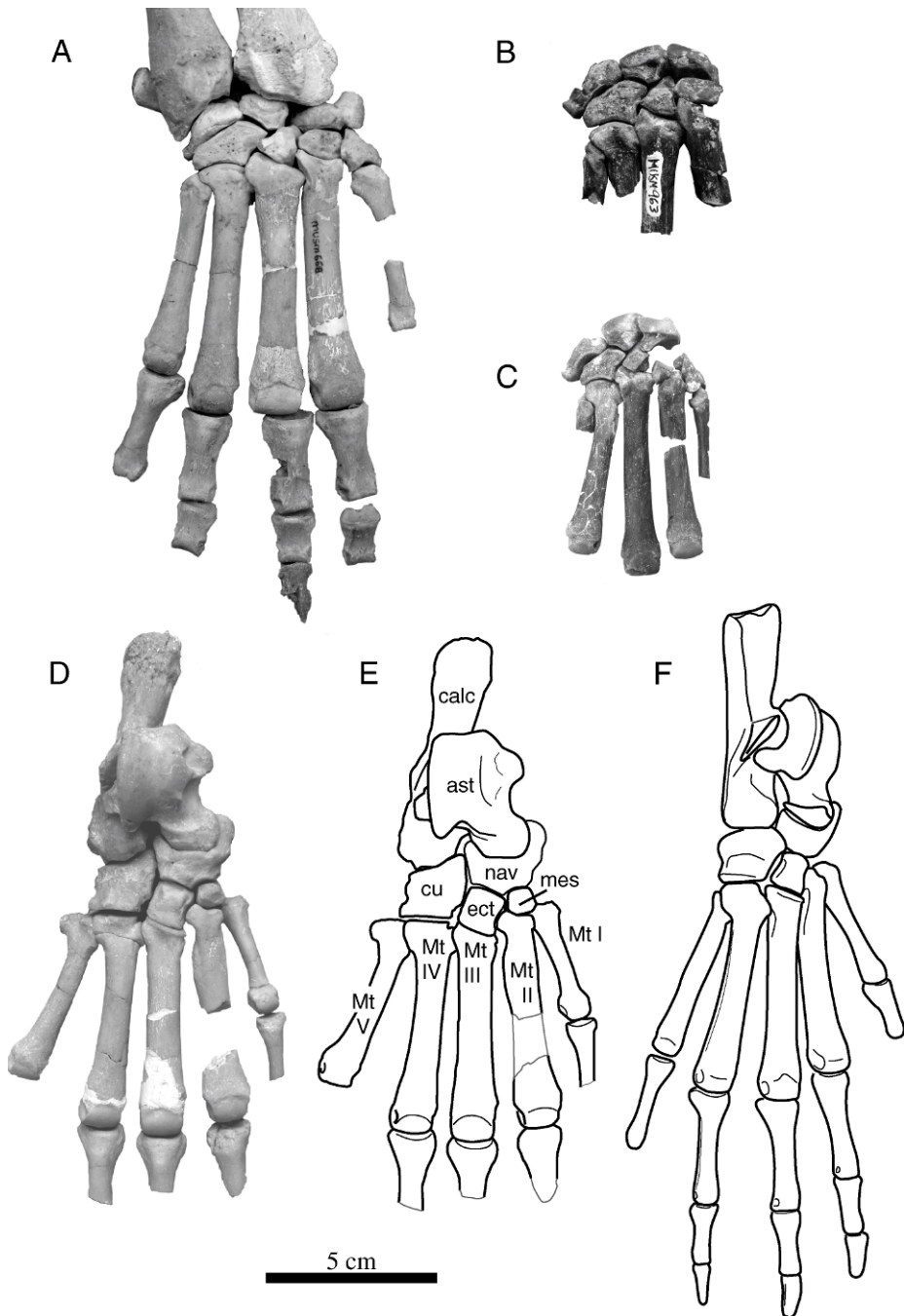


Fig. 8. Trachytheriine autopodia. **A**, Nearly complete right manus of cf. *Trachytherus spegazzinianus* (MUSM 668); **B**, Carpal region of right manus of *Trachytherus* sp. (mid-sized species) (MUSM 963); **C**, right manus (missing digits and trapezoid) of trachytheriine, small indeterminate species, (MUSM 965); **D**, right pes (missing digits) cf. *Trachytherus spegazzinianus* of Moquegua (MUSM 668); **E**, line drawing of *Trachytherus* pes; and **F**, line drawing of *Eutypotherium lehmannnitschei* of Laguna Blanca, Chubut, Argentina (drawn from AMNH 14963, cast of a Museo de La Plata specimen).

However, the phalanges of *Moqueguahippus* differ from those mentioned in that the planter surface is solidly ossified such that the right and left distal ends are fused to one another on the planter side. These phalanges of *Moqueguahippus* are also more robust than those of *Trachytherus*.

SUBORDER TYPOTHERIA ZITTEL, 1892

FAMILY MESOTHERIIDAE ALSTON, 1876

Mesotheriids are a distinctive clade of notoungulates that have a rodentlike incisive battery and hypsodont to hypselodont cheek teeth. They were generally sheep-sized animals and, where known, their postcranial skeletons were modified for strength, such that they have been characterized as digging animals (Shockey et al., 2007).

The monophyletic Mesotheriidae traditionally has been divided into the generally older trachytheriines, of uncertain monophyly, and the generally younger, more diverse, and monophyletic mesotheriines (Cerdeño and Montalvo, 2001; Croft et al., 2004; Flynn et al., 2005).

SUBFAMILY TRACHYTHERIINAE AMEGHINO, 1894

We recognize three distinct taxa of Trachytheriinae mesotheriids from Moquegua. Curiously, none are referable to the common *Trachytherus alloxus* from the nearby and contemporaneous Salla beds of Bolivia.

The recognition of three mesotheriid taxa is based primarily upon the size discontinuities among the postcranial elements, which for convenience we refer to as the large, midsize, and small trachytheriine. The midsize taxon is represented by a nearly complete skull (see Shockey et al., 2006: fig. 2), a detailed description of which will be provided with its formal naming as a new species of *Trachytherus*. For now it will suffice to note a few characteristics that exclude it from the monophyletic Mesotheriinae, such as having a complete upper dentition and root formation of the premolars and M1. The other two taxa are known by postcranial elements, which are very similar to those of other mesotheriids (see Shockey et al., 2007). Where known, Trachytheriinae postcranials are similar to

TABLE 4
Measures of Postcranial Elements (mm) of cf. *Trachytherus spegazzinianus*, MUSM 668, from Cerro Mono, Moquegua

Element	Length	
Calcaneum (length)	69.0	
Tuber calci (midshaft width)	13.1	
Calcaneum width (with sus)	26.9	
Astragalus (proximodistal)	38.7	
Astragalus (trochlear width)	18.8	
Astragalus (width max)	31.0	
Astragalar head (transverse)	16.3	
Astragalar head (dorsoplant)	12.7	
	Length	Width
Mt I	32.7	11.5
Mt II	—	10.7
Mt III	62.8	13.0
Mt IV	61.5	11.7
Mt V	54.5	15.0

those of mesotheriine mesotheriids (Shockey et al., 2007). However, the fusion of the ischium to the sacrum may be a synapomorphy for the Mesotheriinae, as such occurs in the two taxa in which it is known (*Plesiotypotherium* and *Mesotherium*), but is absent in *Trachytherus alloxus*. Such is also absent in the large mesotheriid of Moquegua (see below).

Trachytherus cf. *T. spegazzinianus*
Ameghino, 1889

Figure 8; tables 4 and 5

MATERIAL: MUSM 668, a partial skeleton preserving much of the limbs, including both hands and feet, and both radii. Other elements are less well preserved and include fragments of the humerus, axial skeleton, pelvis, tibia, and fibula.

LOCALITY: Eusebio Díaz and Mario Urbina discovered the partial skeleton MUSM 668 within the upper Moquegua Formation, on a ridge a half a kilometer south of the western summit of Cerro Mono (fig. 1: g on the map).

DESCRIPTION: The skeletal material of the Cerro Mono mesotheriid is so similar to that of *Trachytherus alloxus* from Salla that just a brief description of the new material is needed

TABLE 5
Comparative Measures (mm) of Astragalus and Metacarpals of Mesotheriids of Moquegua

Taxon	Specimen	Astragalar length		Trochlear width		Max width
<i>cf. T. spegazzinianus</i> (large species)	MUSM 668	37.0		16.4		31.5
<i>Trachytherus</i> (midsize)	MUSM 961	30.8		14.0		(25.5)
<i>Trachytherus</i> (midsize)	MUSM 962	—		13.4		24.5
<i>Trachytherus</i> (midsize)	MUSM 966	29.0		13.5		24.3
<i>T.?</i> sp. indet. (small)	MUSM 967	(23)		10.0		18.5
Mc lengths	Specimen	Mc I (length)	Mc II (length)	Mc III (length)	Mc IV (length)	Mc V (length)
<i>cf. T. spegazzinianus</i> (large species)	MUSM 668	—	76	75.5	72.9	60.3
<i>T.?</i> sp. indet. (small)	MUSM 965	—	—	56.5	48.1	—
Mc proximal widths	Specimen	Mc I (width)	Mc II (width)	Mc III (width)	Mc IV (width)	Mc V (width)
<i>cf. T. spegazzinianus</i> (large species)	MUSM 668	10.5	14.1	16.9	16.6	10
<i>Trachytherus</i> (midsize)	MUSM 963	—	—	13.0	13.6	8.0
<i>T.?</i> sp. indet. (small)	MUSM 965	—	10	10.5	11.8	6.2

here. However, until now, no pes of any mesotheriid has ever been described, so we provide some details of it below. In general, the animal of Cerro Mono differs from *T. alloxus* in its larger size and more gracile features. Due to its slightly larger size we provisionally refer it to *T. spegazzinianus* (see Billet et al., 2008, for the subtle differences between *T. spegazzinianus* and *T. alloxus*). Until the recent naming of *T. alloxus* Billet et al., 2008, the mesotheriid of Salla had been referred to *T. spegazzinianus*. Thus, references regarding our discussion of *T. alloxus* (e.g., Sydow, 1988; Shockey et al., 2007) identify the trachythere of Salla as *T. spegazzinianus*.

At 170 mm in length, the radius of the Cerro Mono mesotheriid is a little longer than the largest radius known for *T. alloxus* from Salla (Shockey et al., 2007). Aside from being slightly more gracile than those referred to *T. alloxus*, it is similar to the Salla specimens in general form, having a wide proximal region with a sigmoidal articular surface for the capitulum of the humerus as well as lateroventral facets for articulation with the ulna and probably an elbow sesamoid, as occurs in *T. alloxus* (Shockey et al., 2007), as well as the toxodontid *Nesodon* (Scott, 1912: pl. 25.8). The distal radius of MUSM 668 clearly

illustrates four distinct grooves for tendons of the wrist and digit extensor muscles (fig. 8A).

Both hands are preserved. Although the shaft of the pollex is broken on both right and left sides, the manus is unambiguously pentadactyl, as in *T. alloxus* of Salla (Shockey et al., 2007).

Based on the deep groove for the tendon of the flexor hallicis longus on the astragalus of *Trachytherus*, Ameghino (1905) predicted the presence of the great toe (hallux) in the animal. The pes of MUSM 668 proves him correct (fig. 8D, E). Although Mt I is the shortest metatarsal, it is not an insignificant element. It is over half the length of Mt III–V and its proximal width is similar to those of the remaining metatarsals (table 4). The proximal articular surface of Mt I is rather robust, but the entire joint could not be observed since the entocuneiform was not preserved. The other metatarsals (Mt II–V) are subequal in length, but Mt V is thinner than Mt II–IV. An articular facet on the proximolateral surface of Mt II illustrates that there was some articulation between Mt I and Mt II. Mt II has a lateral process that overlaps Mt III and the distal portion of the ectocuneiform, giving it a secure joint with these elements. Mt III and IV articulate with the ectocuneiform and cuboid,

respectively, at the same level. The articulation between Mt III and IV was accomplished by a distinctive spheroid process on the dorsotibial side of Mt IV inserting into a concave facet of Mt III. An additional articulation occurs between Mt III and Mt IV at the planter region of the metatarsals. This articulation is flatter than the ball-and-socket articulation at the dorsal region. An overlapping process on the proximofibular side of Mt IV provides a dorsoplantarly deep receptacle for the proximal surface of the Mt V. The most noteworthy feature of Mt V is a robust lateral process that appears to have provided a significant lever arm for abduction.

All five proximal phalanges were in articulation with the metatarsals, however, their distal ends were not preserved. Enough of these elements are present to illustrate that all were relatively long, even the first digit (see fig. 8 D, E). No medial or distal phalanges were in articulation with either pes, but some of the ungual phalanges associated with the skeleton likely belonged to the pes as they were unlike those associated with the manus and unlike those known for the hand of *T. alloxus* or *Mesotherium* (Shockey et al., 2007). Those suspected of being from the pes were more clawlike (sharp with little dorsoplantar compression) and lacked the longitudinal fissure observed in the ungual phalanges of the manus.

The proximal tarsals of *Trachytherus* have been described in detail elsewhere (Ameghino, 1905; Sydow, 1988; Shockey et al., 2007), so we note here only distinctive features of the astragalus, including asymmetric trochlear ridges, a separate and well-developed groove for the tendon of the digital flexor, the moderately long and constricted astragalar neck, and the subspherical head. The navicular has a deeply concave facet for articulation of the spheroid head of the astragalus. It is buttressed on the medial side by a proximal process, like that of the tyotheres *Hegetotherium* and *Interatherium* (Sinclair, 1909) and *Prohegetotherium* (Shockey and Anaya, 2008).

Whereas the articulation between the astragalus and navicular is a ball-and-socket joint (the astragalar head forming the “ball” and the deep concavity of the navicular

forming the “socket”), the calcaneal-cuboid joint forms a sliding articulation. This permitted considerable rotation of the middle ankle joint, suggesting some capabilities for inversion of the foot.

Trachytherus sp. (medium size)

Figure 8B; table 5

MATERIAL: MUSM 350, skull (damaged basicranium) and mandibles (Shockey et al., 2006: fig. 2); MUSM 963, left and right partial manus; and astragali MUSM 961, 962, and 966.

LOCALITY: All from the summit of Cerro Pan de Azúcar, near the point where the skull and jaws (MUSM 350) was found (fig. 1: c on the map).

DESCRIPTION: A variety of postcranial elements referable to *Trachytherus* were found alongside the skull (MUSM 350), as well as an m3 of a different individual of *Trachytherus* that are referable to this midsize mesotheriid. Most of these elements likely do not represent the same individual as MUSM 350 since they appear to be from ontogenetically younger individuals. We refer the partial manus of MUSM 963 (fig. 8B), as well as some tarsals found nearby, to this unnamed taxon. A smaller mesothere manus (MUSM 965; fig. 8C) may also pertain to this taxon, but we do not refer it to this taxon since it is so small that it likely represents a different species (see below).

The manus of this midsize trachytheriine (fig. 8B) is similar to that of cf. *T. spegazzinianus* from Cerro Mono of Moquegua (see fig. 1: g on map for locality; fig. 8A for the manus) and the manus of *T. alloxus* from Salla (Shockey et al., 2007; identified there as *T. spegazzinianus*). We note the unfused distal radius and ulna of MUSM 963, which indicates that even though it was found in close proximity to the skull (MUSM 350), it represents a different, ontogenetically younger individual, whereas the complete eruption of the M3 and the significant dental wear indicates that the MUSM 350 is a mature individual. The manus MUSM 963 is nearly identical to those of *T. spegazzinianus* and the small indeterminate species discussed below (fig. 8 A, C), save for its size intermediate

between the two. Also, since neither the trapezoid nor Mc I were recovered, we cannot assert that the manus of this midsize taxon was pentadactyl like *T. alloxus*, cf. *T. spegazzinianus* (fig. 8A), and the small indeterminate species, but we note that even the Pleistocene *Mesotherium* had five digits on its manus (Serres, 1867; Ameghino, 1891; Shockey et al., 2007.)

CF. TRACHYTHERIINAE

Small indeterminate species

Figure 8C; table 5

MATERIAL: MUSM 965 right and left manus, the right being nearly complete, while the left is missing the trapezoid and trapezium and the metacarpals are fragmentary (fig. 8C); MUSM 966 astragalus.

LOCALITY: Collected in the upper Moquegua Formation, at the summit of Cerro Pan de Azúcar, near the skull of the midsize *Trachytherus* sp. (MUSM 350) (fig. 1: c on the map).

DESCRIPTION: Fragments of postcranial elements of a very small trachytheriine were found near and among broken remains of specimens of the midsize species of *Trachytherus*. These may represent small individuals of that taxon or (more likely) may indicate that a third trachytheriine species was present. These distinct elements do not represent an ontogenetic difference between the manus of MUSM 965 and that of MUSM 963 from the same spot, since both are at the same stage of development (fused metacarpals and unfused distal radii and ulnae).

The sample size is too small to be conclusive, but we note several size discontinuities between these smallest indeterminate trachytheriines, the midsize *Trachytherus* sp. and cf. *T. spegazzinianus* (table 5). Postcranial elements referred to the midsize taxon have linear dimensions generally 15% to nearly 30% greater than the same regions of the small, indeterminate trachytheriine. Skeletal elements referred to *T. spegazzinianus* are much larger than both this diminutive trachytheriine and the midsize taxon.

We figure the left manus of this small trachytheriine and note its close similarity to

the manus of both the large (cf. *T. spegazzinianus*) and the midsize taxon (fig. 8) as well as that of *T. alloxus* (Shockey et al., 2007). These also are very similar to the manus of the Pleistocene mesotheriine *Mesotherium* (Ameghino, 1891; Shockey et al., 2007).

DISCUSSION

AGE OF THE MOQUEGUA LOCALITIES: The Sugarloaf ash provides a high-precision ^{40}Ar - ^{39}Ar age determination of 26.25 ± 0.10 Ma for the lower part of the upper Moquegua Formation. This is consistent with the ^{40}K - ^{40}Ar ages reported by Tosdal et al. (1981) for stratigraphically higher levels of the upper Moquegua, exposed east of the Moquegua River. Since we recovered fossils within 20 m above and about 10 m below this ash at Cerro Pan de Azúcar, in the lower part of the upper Moquegua Formation, we accept the new high-precision ^{40}Ar - ^{39}Ar age as the best available estimate of the age of the Moquegua Fauna. This places the Moquegua Fauna within the late Oligocene.

Although no paleomagnetic studies have been performed for the Moquegua sequences, the age of 26.25 ± 0.10 Ma indicates that these beds are contemporaneous with fossil-bearing horizons of Salla, Bolivia, which are located just 365 km east of the Moquegua localities, at essentially the same latitude (about S17°10' for Salla and S17°13' for Moquegua). Based on the best-fit composite ^{40}Ar - ^{39}Ar / paleomagnetic correlation of Kay et al., 1998, the fossil-bearing horizons at Salla range from sediments believed to be as old as paleomagnetic chron C10r (28.74–29.40 Ma) to an age less than 25.50 Ma. This interpretation of the ages of the Salla strata suggests that the Moquegua fauna correlates with “stratigraphic unit 3” in the Calabozza Pata region of Salla, which have an estimated age range of 25.66 to 26.55 Ma (Kay et al., 1998). Numerous rodent and notoungulate specimens (including *Trachytherus alloxus*) have been recovered from unit 3 of Salla. Unit 3 antedates the “*Branisella* level” (part of unit 5) from which specimens of the oldest known platyrrhine primate *Branisella* have been recovered (MacFadden et al., 1985; Takai and Anaya, 1996; Kay et al., 1998), the only

level from which primates have been recovered at Salla. Given the ages of both sequences, the fossil-bearing portion of the upper Moquegua Formation is probably older than the “Branisella level,” however, and thus would be older than the first record of primates in South America.

Nevertheless, it would be unwise to conclude much from our failure to recover primate fossils at Moquegua, since many reasonable explanations are possible (e.g., they are there and we missed collecting them; they once lived there, but were not preserved as fossils, because the paleodepositional environments were not appropriate; they were regionally present but locally absent in the Moquegua region, etc.). With the small sample of fossils from Moquegua, the probability of obtaining rare and small specimens is not great. Our efforts at dry screening atop Cerro Pan de Azúcar (at the edge of one of the world’s driest deserts) resulted in the recovery of only fragmentary remains of *Trachytherus* spp., adding nothing new to our faunal list. (The new tiny rodent was recovered by surface prospecting.)

As with the mesotheriids of Moquegua and the notohippid *Moqueguahippus*, the rodent of Moquegua is similar to, but distinct from, a species known from Salla. Both species of *Sallamys* are rather small, but *S. quispea* is smaller and has a relatively (as well as absolutely) smaller dp4. The dp4 of the two species differs also by *S. quispea* having its anterolophid continuous on the labial side, whereas that of *S. pascuali* is continuous on the lingual side (details in description and see also fig. 6).

TRACHYTHERIINAE OF MOQUEGUA: In terms of their geologic age and their position as nearest outgroups to the derived Neogene Mesotheriinae, the various taxa of the possibly paraphyletic assemblage “Trachytheriinae” are of considerable interest for phylogenetic studies. The excellent material of at least three taxa from Moquegua increases knowledge of both the diversity and morphology of trachytheriines. The midsize *Trachytherus* sp. is complete enough to provide particularly significant data on its skull and hand anatomy, while postcranial remains of both a larger (cf. *T. spgazzinianus*) and very small, unnamed

trachytheriine suggest that three trachytheriine species were present in the Moquegua Fauna. The distinction in size among these three taxa is evident in fig. 8 (see also table 5). None of the three Moquegua trachytheriine mesotheriids are referable to *T. alloxus*, a common taxon from the nearby, contemporaneous (at least partly) Salla. Nor are they referable to *T. subandinus*, also known from Deseadan strata from the Departamento de La Paz, Bolivia. Therefore, a total of five species of trachytheriine mesotheriids were present during the late Oligocene in the region that is now southern Perú and western Bolivia (fig. 1). Such species richness, within a limited geographic area, suggests that the region was important in the radiation of these basal mesotheres, a pattern that has been observed for mesotheriine taxa from the Altiplano of Chile as well (Flynn et al., 2002; Croft et al., 2004).

Although the manus of the Pleistocene mesotheriine *Mesotherium* has been known for over 100 years (Serres, 1867; Ameghino, 1891), no mesotheriid pes has been described previously. We note, however, a *Eutypotherium* hind foot cast of a Museo de La Plata specimen in the AMNH collection (AMNH 14963; fig. 8F). Notes associated with the cast indicate that the original specimen was collected with a partial dentition of *Eutypotherium lehmannnitschei* from Laguna Blanca, Argentina (middle Miocene). The casts appear to be of the holotype (MLP 12-1701) of *E. lehmannnitschei* Roth, 1901 (personal commun. with D. Croft). The “lemur-like” morphology of the foot caused an unnamed cataloger to doubt its referral to the associated *Eutypotherium* teeth. Indeed, the primatlike condition of the manus of *Mesotherium* had inspired Ameghino (1891) to suggest a close phylogenetic relationship between typotheres and “prosimians.” Our discovery of the pes of *Trachytherus*, and its similarity to that referred to *Eutypotherium*, removes any doubt about the association of that pes with the teeth of *Eutypotherium*. Inspection of figure 8D–F demonstrates only trivial differences between the pes of the late Oligocene trachytheriine *Trachytherus* and that of the middle Miocene mesotheriine *Eutypotherium* (AMNH 14963, cast). Likewise,

the manus digit formula of mesotheriids is conservative, with the Pleistocene *Mesotherium* also retaining the pentadactyl state (compare our fig. 8A with that of Ameghino, 1891: fig. 10 or Shockey et al., 2007: fig. 5).

The pes of *Trachytherus* is remarkably similar to that of the extant armadillo (*Oryzomys*). Both taxa have asymmetric trochlear ridges of the astragalus with distinctive ball-and-socket astragalar-navicular articulation, and both are pentadactyl (although this is clearly retention of a primitive state). In a multivariate analysis of postcranial elements of over 30 extant mammals of known locomotor habits, mesotheriid notoungulates occupied a similar morphospace as armadillos and other “scratch diggers” (sensu Hildebrand, 1974, 1985). This indicated that *Trachytherus* and *Mesotherium* shared a suite of postcranial characteristics distinct from extant runners, swimmers, and generalists, but like those of extant scratch diggers. Discrete qualitative characters (huge ridges and tuberosities for muscle insertion, fissured phalanges, and robust pelvis) also strongly suggest that mesotheriids were fossorial (Shockey et al., 2007).

ENDEMIC FAUNA OF MOQUEGUA: The Moquegua Fauna is significant for its endemic species. Although the taxonomic diversity recorded from Moquegua is not vast, it is significant that there are several new taxa, considering its proximity to the extensively collected Salla beds, which our study and previous geochronological studies indicate are contemporaneous. For example, hundreds of trachytheriine specimens have been collected from Salla (see Billet et al., 2008: appendix 1 for a partial list of specimens), with numerous skulls curated in several museums (MNHN-Bol, MNHN-Paris, PU, UF, and UATF). None that we know of, however, are conspecific to any of the mesotheriids of Moquegua. Likewise, none of the nothippid specimens from Salla are yet referable to *Moqueguahippus*. Nor are any Salla rodents referable to *Sallamys quispea*, although it appears to be relatively closely related to *S. pascuali* of Salla. Our inspection of dasypodids in the UF and PU collections do not reveal any osteoderms similar to that reported here.

Given the close temporal and geographic proximity of the two Deseadan faunas, we find it a little surprising that none of the four taxa from the Moquegua Fauna, that can be identified to species, are known from Salla (or anywhere else), suggesting that although this fauna was geographically and temporally proximate to the Deseadan Salla Fauna, distinctive paleogeographic and paleoenvironmental conditions probably led to a distinctive regional biotic differentiation for the Moquegua area of coastal Perú.

CONCLUSIONS

This more comprehensive study of the fossil-bearing horizons of the lower portion of the upper Moquegua Formation confirms our initial assessment that the fossils are of a late Oligocene (Deseadan SALMA) age and removes any support for the suggestion of a possible early Miocene age for these beds (Shockey et al., 2006). This late Oligocene age is supported by a new ^{40}Ar - ^{39}Ar age determination for the Sugarloaf ash (26.25 ± 0.10 Ma) and by the many taxonomic similarities of the Moquegua fossils to those of other Deseadan localities. This similarity, however, is only superficial, as we found that none of the taxa that can be identified to species are referable to species described from other Deseadan faunas, not even the nearby and species-rich Salla beds. This difference cannot be attributed to age differences, since the Moquegua fauna is contemporaneous with at least part of the Salla fauna, with the extended depositional interval of Salla strata also having preserved fossils that are both younger and older than those from Moquegua (the ages of various fossil-bearing levels at Salla range from approximately 29 to 25 Ma (Kay et al., 1998).

Trachytheriine mesotheriid notoungulates were an important component during Deseadan time at both Moquegua and in contemporaneous deposits in nearby parts of Bolivia, as indicated by the presence of three coeval taxa at Moquegua and two other trachytheriines in Bolivia (*T. alloxus* and *T. subandinus*; *T. spegazzinianus* is also known at Lacayani, Bolivia [Billet et al., 2008]). We find this extremely high species richness (at least

five contemporaneous species) to be remarkable for such a small area.

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